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Clovis Colonization of Eastern North America: A Phylogenetic Approach

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Abstract Over the past several decades, archaeologists, anthropologists, linguists, and others who study cultural phenomena have begun to appreciate that methods developed to reconstruct the evolutionary, or phylogenetic, relationships among biological taxa can be used to create cultural sequences based on heritable continuity. One method in particular is cladistics, which creates hypothetical statements of relatedness—rendered as trees—based on the model and parameters used. To date, cladistics has been used to create phylogenetic orderings of a wide variety of cultural phenomena, including basketry and other textiles, ceramic vessels, stone projectile points, languages, folk tales, manuscripts, residence patterns, and political organization. Here we lay out the basic method of cladistics and show how it has formed the basis for long-term studies of the colonization of eastern North America during the Early Paleoindian period (ca. 13,300–11,900 calendar years before the present).

Statement of Significance Archaeologists have long used changes in artifact form to measure the passage of time, the supposition being that if the changes are ordered correctly, a historical sequence of forms is created. This is correct, but oftentimes what archaeologists really want to know is which thing produced another thing as opposed to simply preceding it. This is an evolutionary sequence. Over the past several decades, not only archaeologists but also anthropologists, linguists, and others who study cultural phenomena have begun to use a suite of methods that were developed to reconstruct the evolutionary, or phylogenetic, relationships among biological taxa, one of which is cladistics. This marks a return to the questions on which the founding of much of anthropology rests: the writing of cultural lineages. This return is important to the growth and continued health of archaeology and anthropology because a reconstructed phylogeny helps guide interpretation of the evolution of traits in that it generates hypotheses about the lineages in which those traits arose and under what circumstances.

Data availability The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are contained within the paper.

Keywords Cladistics; Clovis; Cultural transmission; Paradigmatic classification; Phylogeny

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Introduction

Using changes in artifact form to measure the passage of time has long been a hallmark of archaeology (Lyman and O'Brien 2006; Lyman, O'Brien, and Dunnell 1997; O'Brien and Lyman 1999). If the changes are ordered correctly, a *historical sequence* of forms is created, although independent evidence is needed to root the sequence—that is, to determine which end of the sequence is older. This is, however, only one kind of a sequence, and throughout our discussion we draw a sharp distinction between it and an *evolutionary sequence*, which is the result of heritability

—one thing related to another in ancestor–descendant fashion as opposed to simply preceding it. Over the past several decades, archaeologists, anthropologists, linguists, and others who study cultural phenomena have begun to appreciate that the methods that were developed to reconstruct the evolutionary, or *phylogenetic*, relationships among biological taxa can be used to create cultural sequences based on heritable continuity. One method in particular is *cladistics*, which, as we explain below, employs a single kind of trait, or character, to create phylogenies (Cap et al. 2008; Lycett, Collard, and McGrew 2007;

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Table 1 Examples of cultural traits examined using phylogenetic methods.

Basketry—Jordan and Shennan (2003, 2005)
Bronze images—Marwick (2012)
European bone points—Riede (2008)
Folk tales and legends—Stubbersfield and Tehrani (2013), Tehrani (2013)
Hominids and stone tools—Foley (1987), Foley and Lahr (1997), Lycett (2007, 2009)
Hunter–gatherer technology—Jordan and Shennan (2009), Prentiss et al. (2014, 2015)
Lactose digestion—Holden and Mace (1997)
Language—Atkinson et al. (2008), Bouckaert et al. (2012), Burenhult, Kruspe and Dunn (2010), Currie et al. (2013), Dunn, Kruspe, and Burenhult (2013), Dunn et al. (2011), Forster and Renfrew (2006), Forster and Toth (2003), Gray and Atkinson (2003), Gray, Drummond, and Greenhill (2009), Gray and Jordan (2000), Greenhill (2011), Greenhill and Gray (2009), Grollemund et al. (2015), Holden (2002, 2006), Holden and Gray (2006), Holden and Mace (2003, 2005), Holden, Mace, and Sear (2003), Holden, Meade, and Pagel (2005), Kitchen et al. (2009), Lee and Hasegawa (2013), Pagel (2009), Platnick and Cameron (1977), Rexová, Frynta, and Zrzavý (2003)
Manuscripts—Barbrook et al. (1998), Cameron (1987), Howe et al. (2001), Robinson and O'Hara (1996), Roos and Heikkilä (2009), Spencer et al. (2004), van Reenen, den Hollander, and van Mulken (2004)
Marriage and residence patterns—Fortunato (2011a, 2011b), Fortunato, Holden, and Mace (2006), Fortunato and Jordan (2010), Jordan et al. (2009), Pagel and Meade (2005)
Mesoamerican pottery—Harmon et al. (2006)
Neolithic pottery—Collard and Shennan (2000)
Neolithic stone plaques—García Rivero and O'Brien (2014)
North American projectile points—O'Brien, Boulanger, et al. (2015), O'Brien, Buchanan, et al. (2015), Darwent and O'Brien (2006), O'Brien, Darwent, and Lyman (2001), O'Brien et al. (2002, 2012, 2014)
Pacific Northwest Coast material culture and customs—Jordan and Mace (2006), Jordan and O'Neill (2010), O'Neill (2013)
Peopling of North America—Buchanan and Collard (2007, 2008a, 2008b), Jennings and Waters (2014)
Political complexity—Currie and Mace (2011), Currie et al. (2010)
Sexual dimorphism—Holden and Mace (1999)
South Pacific pottery—Cochrane (2008), Cochrane and Lipo (2010)
Spread of farming—Gray and Atkinson (2003), Holden (2002, 2006), Holden and Mace (2003)
Turkmen textiles—Buckley (2012), Matthews et al. (2011), Tehrani and Collard (2002, 2009a, 2009b, 2013), Tehrani, Collard, and Shennan (2010)

Mallegni 2007; O'Leary and Gatesy 2008; Smith and Grine 2008). This sets it apart from other ordering methods. To date, cladistics has been used to create phylogenetic orderings of a wide variety of cultural phenomena, including basketry and other textiles, ceramic vessels, stone projectile points, languages, folk tales, manuscripts, residence patterns, and political organization (Table 1).

From a historical perspective, there appear to be several reasons for increased interest in phylogenetic methods as a means of investigating cultural diversity, perhaps the most important of which is a heightened awareness among social and behavioral scientists of parallel issues in evolutionary biology (e.g., Mace and Pagel 1994; Mesoudi, Whiten, and Laland 2004, 2006; O'Brien and Lyman 2003; Pagel 1999) and a willingness to see human culture as an inheritance system in which variation arises from both deliberate invention and imperfect copying (Eerkens and Lipo 2005; Henrich 2001; Henrich and Boyd 1998; Henrich and Broesch 2011; Lycett 2009; Mesoudi and Lycett 2009). The latter point means that cultural transmission is as legitimate a mechanism for creating phylogenetic relationships as genetic transmission is (Grandcolas and Pellens 2005; Mace and Jordan 2011; O'Brien and Lyman 2000, 2002a).

In more precise terms, cultural phylogenists recognize that both cultural and biological transmission play significant roles in the evolution of such things as stone-tool lineages. Stone tools were at one time parts of human phenotypes in the same way that shells, teeth, and fossilized bones were. Whether a tooth represents one or multiple genes—replicators

—is as yet unknown, but this does not hinder the efforts of paleobiologists to determine and explain the evolutionary histories of the organisms whose phenotypic hard parts they study (O'Brien and Holland 1995). Artifacts are not replicators; they are what get replicated. Cultural traits conceived of as ideas held in the mind of individuals are the replicators that are transmitted; cultural learning is both the transmission mechanism and the source of variation that results from transmission errors and recombination (Lyman and O'Brien 1998).

It is difficult to overemphasize that cladistics creates *hypothetical* statements of relatedness—rendered as trees—based on the model and parameters used (Archibald, Mort, and Crawford 2003), not irrefutable statements of precise phylogenetic relationships. Riede (2011, 799) emphasizes that point with respect to the output of cultural phylogenetics: “a given phylogeny constitutes a quantitative hypothesis of the historical relatedness among the chosen units of analysis.... Such hypotheses can then be evaluated statistically and in relation to external datasets, such as stratigraphic, geographical or radiocarbon dating information.”

Critics of cultural phylogenetics have consistently overlooked this point, arguing that cultural phylogeny is nearly impossible to reconstruct because of the nature of cultural evolution (Bateman et al. 1990; Dewar 1995; Hornborg 2005; Moore 1994; Tëmkin and Eldredge 2007; Terrell 2004). They view cultural evolution as a different kind of process from biological evolution, with a faster tempo and a different mode—horizontal transmission—that creates reticulation, thus

eradicating most or all traces of phylogenetic history and reducing the cultural landscape to little more than a blur of interrelated forms. It should come as no surprise, however, that “cultures do not always behave like species” (Ross, Greenhill, and Atkinson 2013) and that cultural evolution probably is, in most respects, faster than biological evolution (Perrault 2012). With cultures we expect even higher rates of horizontal transmission than with biology (Boyd et al. 1997), but do higher rates automatically discount the applicability of cladistics for creating testable hypotheses of cultural phylogeny? The answer is a resounding “no.” For one thing, biological evolution can involve not only reticulation (Endler 1998), where between-species hybridization might be as high as 15–25% in plants and as high as 10% in animals (Mallet 2005), but also cospeciation (Page 2003) and lateral (horizontal) gene transfer—the physical transfer of genetic information from one organism to another, preexisting organism (Dagan and Martin 2007), including between bacteria and eukaryotes (Dunning Hotopp et al. 2007).

Despite these “problems,” biologists have not abandoned the use of phylogenetic trees. Rather, they admit that the history of life is messy (Bell et al. 2010) and move on. Biologists recognize that they deal with subtrees of the “real” tree of life and that those subtrees are, again, nothing more than models, or hypotheses. Cultural phylogenists have recognized the same thing (Collard, Shennan, and Tehrani 2006a, 2006b; Muscio 2010). As Velasco (2012) points out, the significant question is not whether a particular history is a tree but rather how well a tree-like model depicts that history. Thus, a phylogenetic tree is “either useful or useless (in terms of reflecting the character patterns), rather than true or false (in terms of reflecting the course of phylogeny)” (Skála and Zrzavý 1994, 311–312).

Part of the misunderstanding critics have might stem in part from failure on the part of cultural phylogenists to make clear the distinction between methods of phylogenetic inference—“tree-building” methods—and phylogenetic comparative methods, which rely on the trees to understand patterns of descent in order to examine the distribution of adaptive (functional) features (O'Brien et al. 2013). Together, the methods are based on the “logical proposition that given data about the present distribution of traits across taxa and knowledge about the historical relationships between these taxa, it is possible to infer what the traits were like in the past and how they have changed to give rise to their present distribution” (Currie and Mace 2011, 1110). The modern comparative method is designed to escape what has become known as “Galton’s problem”: Comparative studies of adaptation are ambiguous if the possibility of a common origin of the supposedly adaptive features under examination cannot be ruled out (Lycett 2008; Mace and Pagel 1994). This requires a working knowledge of the phylogeny of units included in an analysis—a statement that applies equally to cultural

phenomena and biological taxa. It makes little sense, for example, to talk about certain projectile-point shapes being “adapted” for particular kinds of environment/prey (Buchanan, O'Brien, and Collard 2014; Buchanan et al. 2011; O'Brien, Boulanger, et al. 2015) if we cannot rule out homology as the cause of similarity.

Despite a growing appreciation for cladistics as a useful tool for understanding the evolutionary history of cultural phenomena, there are still occasional lapses in methodological rigor when it comes to applications. This is not surprising, given that the approach (1) was developed outside of anthropology and archaeology, (2) is still not a routine topic in graduate education, and (3) continues to evolve. To that end, our goal here is to outline the basics of cladistics, focusing attention on its underlying logic, which is distinctly different from that underlying other grouping methods that use similarity to join like with like. Cladistics is interested only in similarity that is the product of evolutionary divergence (*homology*) as opposed to convergence (*analogy*). We then turn attention to how cladistics constructs phylogenetic trees, dividing the process into five steps: (1) generating a character-state matrix; (2) establishing the direction of evolutionary change in character states; (3) constructing branching diagrams of taxa; (4) generating an ensemble tree; and (5) assessing the strength of the tree. We stress that our discussion of cladistics is not intended to replace standard texts on the subject (for readable accounts see Brooks and McLennan [1991], Kitching et al. [1998], Lipscomb [1998], and Williams and Knapp [2010]; for an archaeological account, see O'Brien and Lyman [2003]); rather, it is intended as a primer to the logic behind, and the key methodological elements of, cladistics.

We explore each of these steps in more detail by presenting a series of related cladistic analyses we and our colleagues have conducted to examine the colonization of eastern North America during the Early Paleoindian period (ca. 13,300–11,900 calendar years before the present [calBP]). We draw on several previous discussions for background (e.g., O'Brien, Boulanger, et al. 2015; O'Brien, Buchanan, et al. 2015; O'Brien, Darwent, and Lyman 2001; O'Brien and Lyman 2003; O'Brien et al. 2012, 2014), expanding them substantially in light of new work. Our intent is to show that phylogenetic orderings are tools that can be used to address larger issues as opposed to being analytical end points. Here, these issues include the pathways and rates of eastern North American colonization and how those factors influenced cultural transmission within and among Paleoindian groups.

Cladistics and Heritable Continuity

The notion that similarity among cultural phenomena can be used to indicate heritable continuity actually originated with the use of the comparative method in linguistic studies of the late eighteenth and early

nineteenth centuries (Leaf 1979; Platnick and Cameron 1977). As Boas (1904, 518) noted, "owing to the rapid change of language, the historical treatment of the linguistic problem had developed long before the historic aspect of the natural sciences was understood. The genetic relationship of languages was clearly recognized when the genetic relationship of species was hardly thought of. ... No other manifestation of the mental life of man can be classified so minutely and definitely as language. In none are the genetic relations more clearly established." Boas was speaking metaphorically about the "genetic relationship of languages," but his logic was unassailable: Linguistic similarity is the result of transmission and heritable continuity. In modern terms, language is a "culturally transmitted replicator" (Pagel 2009). It is during the transmission process that change occurs, such as in the loss or gain of words or changes in meaning and sound. These are not simple metaphorical analogues of biological features; rather, they are products of the same kinds of mechanisms that create and maintain genetically based variation in organisms (O'Brien and Lyman 2003).

Although culture historians of the twentieth century regularly referred to general processes of cultural transmission—Boas (1911:809), for example, noted that "we must investigate the innumerable cases of transmission that happen under our very eyes and try to understand how transmission is brought about"—they rarely were explicit about *what* was being transmitted or why this might be important (Lyman, O'Brien, and Dunnell 1997). Most often they relied on ethnologically documented mechanisms such as diffusion to account for typological similarities in the archaeological record. Willey (1953, 363), for example, noted that "typological similarity is an indicator of cultural relatedness," but lost was the fact that this axiom falls prey to a caution raised by palaeobiologist George Gaylord Simpson (1961), using monozygotic twins as an example: They are twins not because they are similar; rather, they are similar because they are twins.

In systematic biology in the 1940s and 1950s, formal similarity was used to create *evolutionary taxonomies* (e.g., Dobzhansky 1951; Mayr 1942; Simpson 1945), which were intended to reflect not only patterns of ancestry and descent but also the degree of divergence among taxa. Evolutionary taxonomy was based on the axiom that similarity of phylogenetically related organisms is a result of replication through genetic transmission. Over time, because of transmission errors, mutation, and/or recombination, the organisms comprising a population (or species) change. Despite close adherence to this axiom, evolutionary taxonomies were often problematic because the two features of the evolutionary process that were being shown—pattern of descent and degree of divergence—did not always follow the same patterns and rates (e.g., Eldredge and Gould 1997; Gould and Eldredge 1993). The end result was widespread

subjectivity, with each systematist arguing for his or her own idiosyncratic taxonomy.

Overall similarity in terms of formal characters, or traits, was used to group like with like in descending order of specificity, but overlooked was the notion that there were different kinds of formal similarity, each created by different processes. Biologists were not ignorant of the differences between homologous and analogous characters—the former the result of genealogy and the latter of parallelism or convergence—and they correctly tried to ignore analogous characters and focus only on homologous characters in their taxonomies. As a simple example of the difference between the two kinds of traits, consider taxa with wings and vertebrae. Birds and bats both have wings, and those characters share properties in common, yet we classify birds and bats in two widely separate taxonomic groups because birds and bats are only distantly related phylogenetically: The two large groups diverged from a common vertebrate ancestor long before either one of them developed wings. Therefore wings are of no utility in reconstructing lineages because they evolved independently in the two lineages after they diverged. Conversely, all mammals have a vertebral column, as do animals placed in other categories. The presence of vertebrae is one criterion that we use to place organisms in the subphylum Vertebrata. The vertebral column is a homologous character shared by mammals, birds, reptiles, and some fishes, and it suggests that at some remote time in the past the organisms in these taxa shared a common ancestor.

Culture historians and ethnologists tried to make the same kind of distinction. Kroeber (1931, 151), for example, noted that "the fundamentally different evidential value of homologous and analogous similarities for determination of historical relationship, that is, genuine systematic or genetic relationship, has long been an axiom in biological science. The distinction has been much less clearly made in anthropology, and rarely explicitly, but holds with equal force." Kroeber (1931, 151) went on to imply that a "true homology" denoted "genetic unity," arguing that

There are cases in which it is not a simple matter to decide whether the totality of traits points to a true [genetic, homologous] relationship or to secondary [analogous, functional] convergence. ... Yet few biologists would doubt that sufficiently intensive analysis of structure will ultimately solve such problems of descent. ... There seems no reason why on the whole the same cautious optimism should not prevail in the field of culture; why homologies should not be positively distinguishable from analogies when analysis of the whole of the phenomena in question has become truly intensive. That such analysis has often been lacking but judgments have nevertheless been rendered, does not invalidate the positive reliability of the method. (Kroeber 1931, 152–153)

Despite recognizing the importance of homologous features in tracing descent, biologists and anthropologists

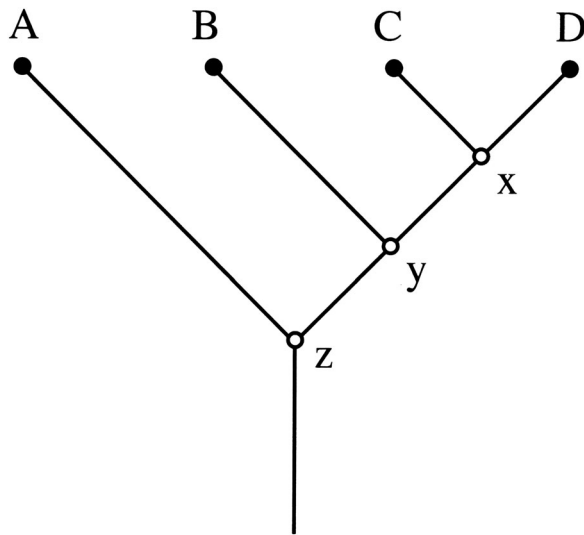


Figure 1 A phylogenetic tree showing the historical relationship of four taxa (A–D) and three ancestors (x–z). Based on a certain character-state distribution (not shown), taxa C and D are more similar to one another than either is to any other taxon. Also, taxa B, C, and D are more similar to each other than any of the three is to Taxon A. Related taxa and their ancestors form ever-more-inclusive groups, or clades: C + D + x is one clade; B + C + D + y is a second; and A + B + C + D + z is a third.

alike ignored the fact that there are different kinds of homologous characters and that it matters greatly how those different kinds of characters are handled during analysis (see below). Another complication was the fact that despite the recognized distinction between homology and analogy, it often was difficult to label a specific character found in two or more taxa as a homologue or analogue without knowing the phylogenetic history of the taxa—the very thing the characters were being used to construct. Thus an alternative to evolutionary taxonomy made its appearance in the 1960s—*numerical taxonomy*, or *phenetics* (Mayr 1981), which clusters objects or groups of objects on the basis of a large number of morphometric characters (Sokal and Sneath 1963). The approach side-stepped the homology–analogy issue by incorporating any and all characters into analysis, but many evolutionary biologists ignored it for the simple reason that it overlooked phylogeny in favor of producing “natural” groups (Hull 1988).

In the late 1940s German entomologist Willi Hennig devised a phylogenetic method that has come to dominate other approaches—what he termed *phylogenetic systematics* (Hennig 1950) but which in the years following publication of his treatise in English (Hennig 1966) came to be known simply as *cladistics*. Cladistics defines phylogenetic relationships in terms of relative recency of common ancestry: Two taxa are deemed to be more closely related to one another than either is to a third taxon if they share a common ancestor *that is not also shared by*

the third taxon. The evidence for exclusive common ancestry is evolutionarily novel, or *derived*, character states.

For example, Figure 1 shows a *cladogram*, or *phylogenetic tree* (we use the terms interchangeably), that classifies four taxa. It tells us that based on a certain character distribution, taxa C and D are more similar to one another than either is to any other taxon. It also says that taxa B, C, and D are more similar to one another than any of the three is to Taxon A. We know that taxa A–D evolved from ancestral taxa, although at this point we know little or nothing about those ancestors except that with respect to certain characteristics taxa C and D look more like their immediate common ancestor (x) than they do the one (y) that unites them with Taxon B. Likewise taxa B, C, and D look more like their common ancestor (y) than they do the one (z) that unites them with Taxon A. In cladistics, convention is to place *nodes* at the points where branches meet and to refer to the nodes as *ancestors* that produced the terminal taxa (those at the branch tips). In our tree, taxa C + D, together with their hypothetical common ancestor (node x), form a monophyletic group, or *clade*. Taxa D + C + B, together with their common ancestor (node y), form another, more inclusive clade, and taxa D + C + B + A, together with their common ancestor (node z), form yet another, and the most inclusive, clade.

One common misconception is that the interior nodes—“ancestors”—are somehow “real.” They are not—hence our use of the term “hypothetical” above—and in fact, ancestors play no analytical role in cladistics because we can never be sure exactly what produced what. We know that taxa do not necessarily die when they produce offspring. For example, Taxon z in Figure 1 did not die when it produced Taxon A and Taxon y, so we show the ancestor as a sister taxon (A). It is simply a matter of convention to circumvent the illogical problem of having parents die when offspring are born (Sober 1988).

Another series of trees is shown in Figure 2, this time with emphasis on the kinds of characters and character states that one encounters in phylogenetic studies. The trees show the evolution of a projectile-point lineage that begins with Ancestor A. For simplicity, we are tracking only a single character, fluting (the removal of one or more longitudinal flakes from the base of a projectile point in order to thin it), for which two character states are possible, fluted and unfluted. Over time, Ancestor A, which is unfluted, gives rise to two lines, one of which, like its ancestor, is unfluted and the other of which is fluted (Figure 2a). Thus the character state “fluted” in Taxon 2 is derived from the ancestral character state, “unfluted.” In Figure 2b, Ancestor B (old Taxon 2) gives rise to two new taxa, 3 and 4, each of which carries the derived character state, “fluted.” At this point “fluted” becomes a *shared derived* character state, defined as a character or character state shared only by sister taxa and their

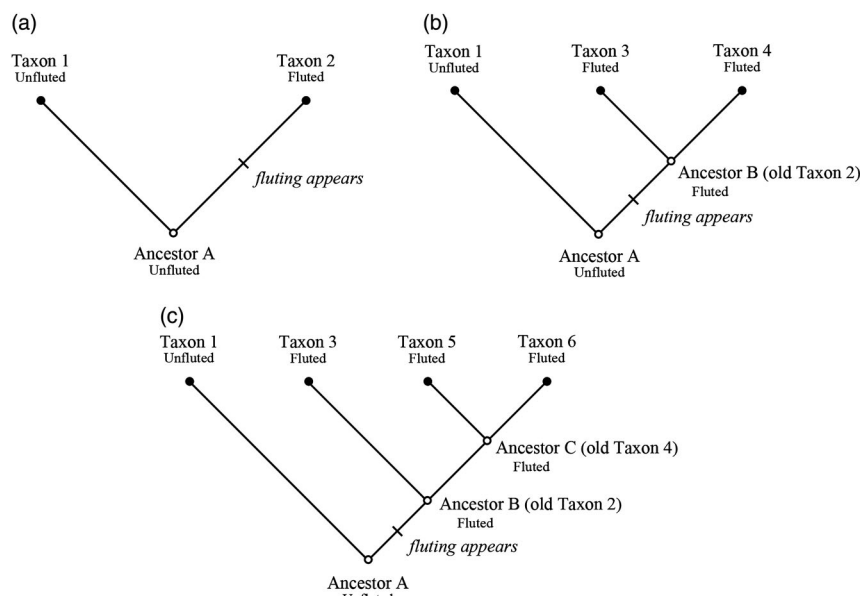


Figure 2 Phylogenetic trees showing the evolution of projectile-point taxa (from O'Brien, Darwent, and Lyman 2001). In (a), fluting appears during the evolution of Taxon 2 out of its ancestral taxon. Its appearance in Taxon 2 is as a derived character state. In (b), Taxon 2 has produced two taxa, 3 and 4, both of which contain fluted specimens. The appearance of fluting in those sister taxa and in their common ancestor makes it a shared derived character state. In (c), one of the taxa that appeared in the previous generation gives rise to two new taxa, 5 and 6, both of which contain fluted specimens. If we focus attention only on those two new taxa, fluting is now a shared ancestral character state because it is shared by more taxa than just sister taxa 5 and 6 and their immediate common ancestor. But if we include Taxon 3 in our focus, fluting is a shared derived character state because, following the definition, it occurs only in sister taxa and in their immediate common ancestor.

immediate common ancestor. Characters in sister taxa that have been inherited from an ancestor more distant than the common ancestor are *shared ancestral* characters. In Figure 2c, in which two descendent taxa have been added, fluting is now a shared ancestral character relative to taxa 5 and 6 because it is shared by three taxa and two ancestors. But relative to taxa 3, 5, and 6, fluting is a derived character state because it is shared by three taxa and their immediate

common ancestor, B. Thus depending on where in a lineage one begins, a trait can be derived or ancestral.

Figure 2 does not show a third kind of character, but it is one that occurs often on phylogenetic trees and, if not recognized, creates false positives in terms of similarity resulting from common ancestry. These are analogues, which in cladistics are referred to as *homoplasies*—similarities resulting from processes other than descent from a common ancestor, such as

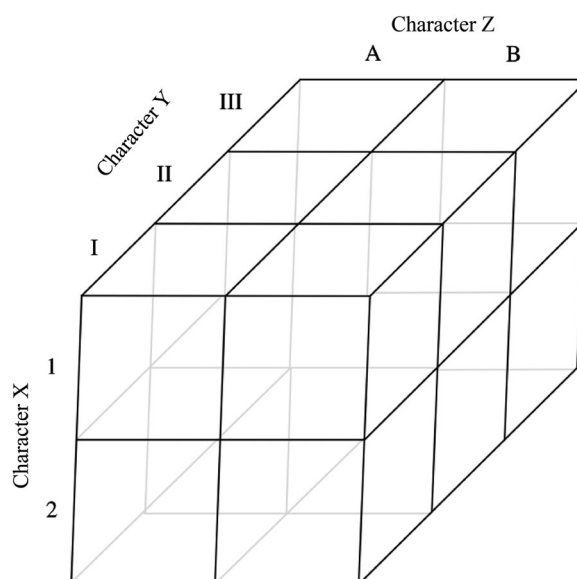


Figure 3 A simple three-dimensional classification system showing the intersection of the character states of each character to create 12 taxa (2 x 3 x 2).

convergence, parallelism, and horizontal transmission between lineages (O'Brien and Lyman 2003; Sanderson and Hufford 1996). Suppose in Figure 2c that the tree is a true depiction of projectile-point evolution. Suppose further that taxa 1 and 6 share a character—say, beveling—that taxa 3 and 5 do not exhibit. We would refer to beveling as a *homoplasious* character—one that arose independently in those two taxa.

Constructing Phylogenetic Trees

In its simplest form, cladistic analysis proceeds via five steps, the end process being the construction of phylogenetic trees that are useful in understanding not only the evolutionary relationships among the taxa being examined but also the evolutionary changes in character states that the taxa exhibit.

Step 1: Generating a Character-state Matrix

The data set used in any cladistic analysis is a matrix that lists the taxa and their character states. The intersection of character states is what defines each taxon. As a simple example, Figure 3 shows a set of 12 taxa defined by the states of three characters: X, Y, and Z. Character X, height, has two states, 1 and 2; character Y, depth, has three states, I, II, and III; and character Z, width, has two states, A and B. The taxa created through the intersections of the various character states are the three-character boxes shown in the diagram—1IA, 1IIA, 2IB, and so on. How do we choose appropriate characters, with appropriateness meaning how well a character performs in allowing us to separate taxa phylogenetically? In other words, how do we know a priori that a particular character will produce a phylogenetic signal? The bottom line is, we don't. In reality, character choice is a classic case of trial and error, with a good measure of experimental evidence and inductive reasoning thrown in. We return to the selection of characters a bit later.

Step 2: Establishing the Direction of Evolutionary Change in Character States

Several methods have been developed to facilitate establishing the direction of evolutionary change in character states (polarity), one of which is outgroup analysis (Maddison, Donoghue, and Maddison 1984). Basic to the method is identifying a close relative of the taxa in the study group (ingroup). The logic is this: Character states exhibited by taxa in the study group but not by the outgroup are, under the principle of parsimony, deemed to be evolutionarily novel with respect to the outgroup states. For example, in Figure 2c, Taxon 1 is an outgroup to taxa 3, 5, and 6. It is important to make clear that analytical use of the term "parsimony" has nothing to do with whether evolution itself is parsimonious. Rather, it has to do with logical argumentation: It is more parsimonious to make as few ad hoc phylogenetic hypotheses as possible (Sober 1983). Lipscomb (1998), among others, makes the useful point that the simplest hypothesis is the one that is most easily defensible.

Moreover, when one is faced with a decision regarding alternative hypotheses, it provides a logical basis for choosing among alternative working hypotheses, which can be especially important in archaeology (e.g., Buchanan and Collard 2007; Lycett 2007, 2009). In other words, parsimony can be important for establishing—objectively, systematically, and quantitatively—what is the most parsimonious scenario from a set of alternative explanations, even when the most parsimonious one seems counterintuitive.

A degree of circularity often is built into outgroup comparison because it presumes that we know a priori that the chosen outgroup is no more closely related to one group than it is to any other group under consideration. In other words, it assumes something about what it is we are trying to discover. This has resulted in observations such as Eldredge and Novacek's (1985, 68) that "cladistics is no panacea. It is hard to do a good piece of systematics research using cladistics. ... The system is logically much more rigorous, requiring every available item of evidence," including (1) the congruence criterion—multiple characters suggesting the same phylogenetic tree (Rieppel 1994); (2) an assumption of parsimony—that particular innovations will appear a minimum number of times (Sober 1988); and (3) independent temporal clues, such as that derived from superposition, to test indications of which character states are ancestral and which are derived (e.g., Donoghue et al. 1989).

Step 3: Constructing Branching Diagrams of Taxa

After the probable direction of change for the character states has been determined, usually through the use of computer programs designed for that purpose—PAUP* (v. 4) (Swofford 1998) was used to create all the trees discussed here—the third step is to construct a branching diagram that shows the phylogenetic relationship of the taxa. This is done by joining the two most derived taxa by two intersecting lines and then successively connecting each of the other taxa according to how they are derived. Again, this is usually done with the assistance of computer programs.

Various methods have been used for phylogenetic inference, each based on different models and each having its own strengths and weaknesses (Archibald, Mort, and Crawford 2003; Douady et al. 2002; Goloboff and Pol 2005; Ogden and Rosenberg 2006; Pol and Siddall 2001; Sober 2004). The one we discuss here, *maximum parsimony*, is based on a model that, as we noted above, seeks to identify the least number of evolutionary steps required to arrange the taxonomic units under study. Parsimony trees are evaluated on the basis of the minimum number of character-state changes required to create them, without assuming a priori a specific distribution of trait changes. Two other commonly used methods, *maximum likelihood* and *Bayesian inference*, are probabilistically based, where the criterion for constructing trees is calculated with reference to an explicit evolutionary model from

which the data are assumed to be distributed identically (Kolaczowski and Thornton 2004). Both methods take into account the uncertainty in a data set, which maximum parsimony does not. Maximum likelihood, for example, asks what the probability is of observing a particular arrangement of data (a tree's topology), given that a particular phylogenetic tree is correct. Bayesian methods estimate the probability that a hypothesis is true—a given tree is correct—given certain observations and model assumptions derived from prior probabilities. Cultural phylogenies that are based on language evolution have relied largely on probabilistic methods (e.g., Currie and Mace 2011; Gray, Drummond, and Greenhill 2009). Those not based on language evolution—archaeological phylogenies, for example, which are more prospective (e.g., Buchanan and Collard 2007, 2008a, 2008b; García Rivero and O'Brien 2014; Lycett 2009; O'Brien, Darwent, and Lyman 2001; O'Brien et al. 2001, 2012)—tend to rely on parsimony.

Ideally, the distribution of character states among taxa will be such that all character-state relationships are congruent, but we have never witnessed such a happy event. Far more likely, a tree will contain multiple character states that show up in lines not related directly through one common ancestor. As discussed earlier, these are referred to as homoplasies. One kind of homoplasy results from character-state reversals, meaning, for example, that character state A changed to state A' and then at some later point in the lineage reverted to state A. We view this kind of homoplasy in biology more as a classification problem, meaning that rarely if ever will precisely the same character state reemerge after it disappears. More likely, the classification system being used makes it appear as if the new character state is a homoplasy. With respect to, say, stone tools, our experience has been that character-state reversals are fairly common (O'Brien and Lyman 2003), as tool

makers experiment with new designs and then abandon them in favor of previous designs. Another kind of homoplasy results from parallelism or convergence—organisms, perhaps because of anatomical and/or environmental constraints (the first the result of common history, the second because of similar environments), independently evolve the same character state. With respect to cultural phenomena, borrowing (horizontal transfer) is a common source of convergence.

Step 4: Generating an Ensemble Tree

The fourth step in a cladistic analysis is to generate an ensemble tree that is consistent with the largest number of characters and therefore requires the smallest number of homoplasies to account for the distribution of character states among the taxa. There are several ways of generating such a "consensus" tree, one of which is to construct a majority-rule tree, which places taxa in their most common positions across the sample of trees (Swofford 1998). The percentage of trees in which the taxa must occur in the same positions can be varied between 50 percent and 100 percent. An example of a 50-percent majority-rule consensus tree is shown in Figure 4. Notice that the G + H + I clade has the same arrangement in two out of the three trees; thus that arrangement is the one shown in the consensus tree. The same is true for the E + F clade. It also holds true for the other four taxa, although it is not as readily apparent. Note also that the middle tree just happens to have the same arrangement of taxa as the consensus tree.

Step 5: Assessing Robustness

How robust are the trees we generate? That is, how well do they approximate the one true phylogeny we assume exists? One determination of robustness is the consistency index (CI), which measures the amount of homoplasy in a data set (Farris 1989b;

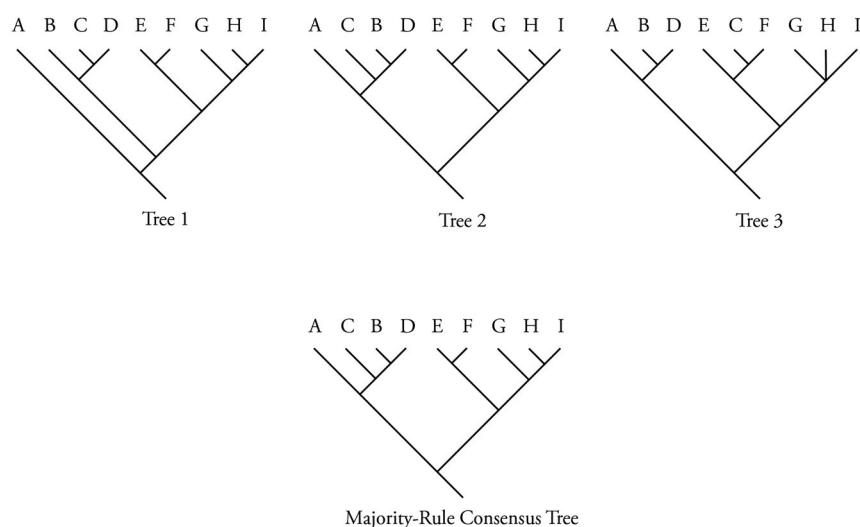


Figure 4 Fifty-percent majority-rule consensus tree based on three trees of equal length (from O'Brien and Lyman 2003).

Goloboff 1991). The index ranges from 0 (complete homoplasy) to 1.0 (no homoplasy) and is calculated by dividing the number of characters in the data matrix by the number of characters on the tree. There are several potential drawbacks to the consistency index, one of which is that the CI value is not independent of the number of taxa. When the number of taxa increases, the CI value will decrease. To overcome some of the problems, Farris (1989a, 1989b) developed the rescaled consistency index and the retention index (RI), the latter of which measures the fit of characters to a cladogram (the ratio of apparent synapomorphy to actual synapomorphy). The RI is calculated as

$$\frac{\text{Max. steps in matrix} - \text{No. of characters on tree}}{\text{Max. steps in matrix} - \text{No. of characters in matrix}}$$

It is difficult to overstate the fact that no phylogenetic index is without its issues (Crema et al. 2014). Nunn et al. (2010) enumerate three general concerns with the CI and RI. First, they were designed to assess the degree of homology in biological data, and increases in rates of evolution can lead to lower homology, i.e. a lower CI or RI. Second, if a large number of traits are borrowed as what Boyd et al. (1997) refer to as a cultural “package,” then parsimony inference should, on average, produce a tree with low homoplasy, albeit one that differs from the history of other cultural or genetic traits and despite the possibility of extensive borrowing. Third, both the CI and RI lack a firm statistical framework for assessing the importance of a particular value. As an example, suppose a set of traits produces a tree with an RI of 0.6. Is that higher than expected? Is it lower than expected? Does it constitute evidence for horizontal or vertical transmission? As Nunn et al. (2010) point out, about all that can be done is to compare values with those obtained from biological traits or systems that have better understood properties (Collard, Shennan, and Tehrani 2006b).

As a way around this conundrum, Nunn and colleagues used a simulation model to test whether the

CI and RI can detect horizontal transmission. They also investigated other variables that might influence the calculations, including rates of evolution, as higher rates should increase homoplasy, thus reducing the indices. They found that the simulations with the highest RI for both the parsimony tree and the true tree created as the basis of the model were characterized by low rates of evolution and low horizontal transmission. Based on this finding, Nunn and colleagues concluded that a high RI is consistent with low horizontal transmission and a high degree of vertical transmission of trait variation. However, they found it difficult to conclude that a low RI is indicative of horizontal transmission, as this is also consistent with high rates of evolution. This important caveat needs to be made explicit in all cultural phylogenetic studies.

An Archaeological Example: Paleindian Colonization of Eastern North America

The exact timing of the colonization of North America is open to question (see below), but what is not in question is the point of origin of the early colonists. Despite a few claims to the contrary (e.g., Stanford and Bradley 2012), the overwhelming archaeological and archaeogenetic evidence indicates that humans entered North America by way of Beringia (Goebel, Waters, and O'Rourke 2008; Kemp and Schurr 2010; Morrow 2014; O'Rourke and Raff 2010; Raff and Bolnick 2014; Raff et al. 2010; Raghaven et al. 2015; Rasmussen et al. 2014; Waters and Stafford 2007) and made their way either south along or near the coast (Erlandson et al. 2007; Fladmark 1979) or through a corridor that ran between the Cordilleran and Laurentide ice sheets (Catto and Mandryk 1990; Mandryk et al. 2001).

With respect to timing, colonizing populations could have entered North America more than 16,000 years ago, but the earliest well-documented human occupation of North America dates several thousand years later. It is marked by bifacially chipped and fluted stone weapon tips known as “Clovis” points,



Figure 5 Clovis points from various North American sites (specimens cast by Pete Bostrom/Lithic Casting Laboratory).

which exhibit parallel to slightly convex sides and a concave base and a series of flake-removal scars on one or both faces that extend from the base to about a third of the way to the tip (Fig. 5) (Bradley 1993; Buchanan and Collard 2010; Morrow 1995; Sholts et al. 2012; Wormington 1957). These points were hafted to spears that were thrust and/or thrown. Clovis points are found throughout the contiguous United States, Alaska, southern Canada, and northern Mesoamerica (Anderson and Faught 1998, 2000; Anderson et al. 2010; Buchanan and Collard 2007, 2010; Buchanan et al. 2012; Goebel, Waters, and O'Rourke 2008; Haynes 1964; Holliday 2000; Prasciunas 2011; Sanchez 2001; Sholts et al. 2012; Smallwood 2012; Waters and Stafford 2007) and date ca. 13,300–12,800 calBP in the West and ca. 12,800–12,500 calBP in the East (Gingerich 2011; Haynes et al. 1984; Haynes 2002; Holliday 2000; Levine 1990).

In light of their wide distribution and time depth, it is not surprising that Clovis points exhibit considerable variation in size and shape (Buchanan, O'Brien, and Collard 2014; Haynes 2013). What might account for the variation? Is it the result of drift—that is, is it random—or is there regional patterning that might suggest an adaptive reason? Buchanan, O'Brien, and Collard (2014) refer to the former as the *continent-wide adaptation hypothesis*, which holds that Clovis groups did not adjust the shape of their points in relation to local environmental conditions (Byers 1954; Haynes 1964; Kelly and Todd 1988; Krieger 1954; Robinson et al. 2009; Sholts et al. 2012; Willey and Phillips 1958) and that variation in shape is the result of cultural drift (Hamilton and Buchanan 2009; Morrow and Morrow 1999). The alternative—the *regional environmental adaptation hypothesis* (Buchanan, O'Brien, and Collard 2014)—posits that Clovis groups adapted their hunting equipment to the characteristics of prey and local habitat, which resulted in regional differences in projectile-point shape (Anderson 1990; Meltzer 1988; Smallwood 2012; Storck and Spiess 1994).

Buchanan and Hamilton (2009) expanded on the distinction between the competing hypotheses. With respect to projectile points, they defined drift as a measurable change in point form because of neutral stochastic processes caused by sampling effects that occur as the result of cultural transmission in finite, naturally fluctuating populations (Neiman 1995; Shennan and Wilkinson 2001). As a consequence of sampling, drift is amplified in smaller populations, where the number of people from whom to copy, and the number of objects or traits to copy, are limited (Bentley and O'Brien 2011). This process is heightened when populations bud off and become isolated from a parent population (Shennan 2000, 2001). This is known as the “founder effect”—smaller populations retain only a limited set of the cultural variation exhibited among the original population, which is then subject to drift. As Atkinson (2011) points out, the founder effect has been used to explain numerous

patterns of variation in cultural replicators, including human material culture (e.g., Diamond 1978; Henrich 2004; Lycett and von Cramon-Taubadel 2008; Rogers, Feldman, and Ehrlich 2009).

In contrast to drift, adaptive modifications can be made to improve the functional performance of projectile points in specific environments. Buchanan and Hamilton (2009) proposed that functional innovations made to Clovis points were the result of *guided variation* (Boyd and Richerson 1985), a combination of unbiased cultural transmission and individual learning within specific environmental constraints. In individual learning, an individual modifies existing behaviors through trial and error to suit his or her own needs. Perhaps a learner obtains the basic behavior from a parent or master and then begins to tinker with it with no influence from other people. He or she then passes the behavior on to others. After acquiring a behavior or tool, the next individual can obtain environmental information about the relative payoffs of alternative skills or tools. If the difference in payoff is clear—not a certainty in most situations (Bentley and O'Brien 2016; Bentley, O'Brien, and Brock 2014; Bentley et al. 2016)—the individual adopts the behavior indicated by the environmental information. For example, in a changeover from closed to open environments it might be beneficial to have improved aerodynamic capabilities of weapons launched through the air (Lipo et al. 2012) when the size of prey included in the diet changes dramatically (Buchanan et al. 2011) or when hunting prey with comparatively thick hides, in which case it might pay to reduce impact-related fractures through the alteration of point shape or hafting arrangements (Cheshier and Kelly 2006; Frison 1989; Hutchings 1997; Musil 1988). If the difference in payoffs is unclear, the individual sticks with the behavior acquired through unbiased cultural transmission (Henrich 2001). This form of learning is called “unbiased” (Boyd and Richerson 1985) because at the population level it approximately replicates the distribution of behaviors from the previous generation.

To begin to make sense of the variation in Paleoindian point form and the processes responsible for it requires that we create phylogenetic orderings of the points in order to separate instances of homology from instances of analogy. There is no assurance that we will in all instances correctly identify which is which, but cladistics offers us the best way forward. In 1999 we began a long-term study of Paleoindian projectile points from across North America (e.g., Boullanger et al. 2015; Buchanan and Collard 2007, 2008a, 2008b, 2010; Buchanan and Hamilton 2009; Buchanan, O'Brien, and Collard 2014; Buchanan et al. 2011, 2012, 2015; Collard et al. 2010; Darwent and O'Brien 2006; Eren, Buchanan, and O'Brien 2015; Eren, Chao, et al. 2016; Eren, Redmond, et al. 2016; Hamilton and Buchanan 2009; O'Brien et al. 2012), with initial phylogenetic emphasis on points from the Southeast (O'Brien, Darwent, and Lyman 2001; O'Brien and Lyman 2000, 2003; O'Brien et al. 2002). We later expanded the

data set to include points from the entire East (O'Brien et al. 2013, 2014). The data sets included Clovis points plus slightly later Early Paleoindian-period point types that date ca. 12,500–11,900 calBP.

Projectile-point Classes

Instead of using common projectile-point types, such as Clovis, as taxa, we used *paradigmatic classification* to create the taxa, which we refer to as *classes*.

Paradigmatic classification has the ability to produce objective, replicable analytical units. In contrast to taxonomic classification, which is the basis for all projectile-point typology (e.g., Justice 1987; Turner, Hester, and McReynolds 2011), paradigmatic classification uses an unordered and unweighted structure of character states to construct classes (Dunnell 1971; O'Brien and Lyman 2000). Although we did not use the term earlier, paradigmatic

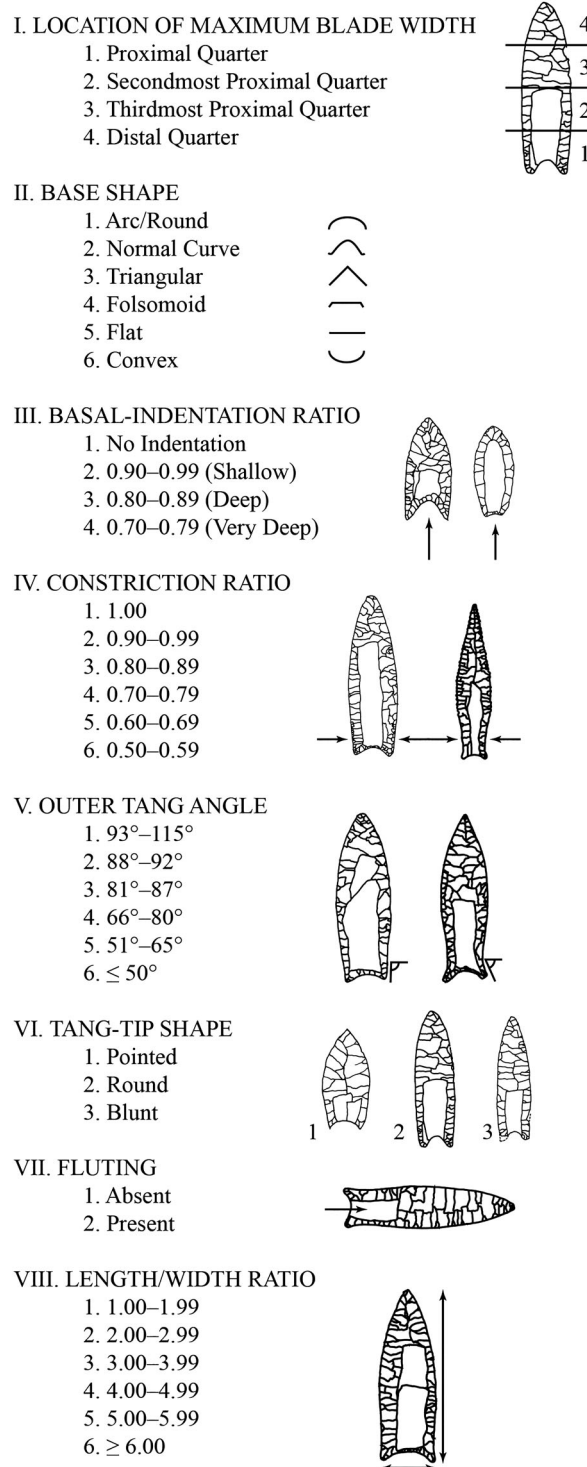


Figure 6 Characters and character states used in the analyses of Paleoindian projectile points from eastern North America (from O'Brien et al. 2014).

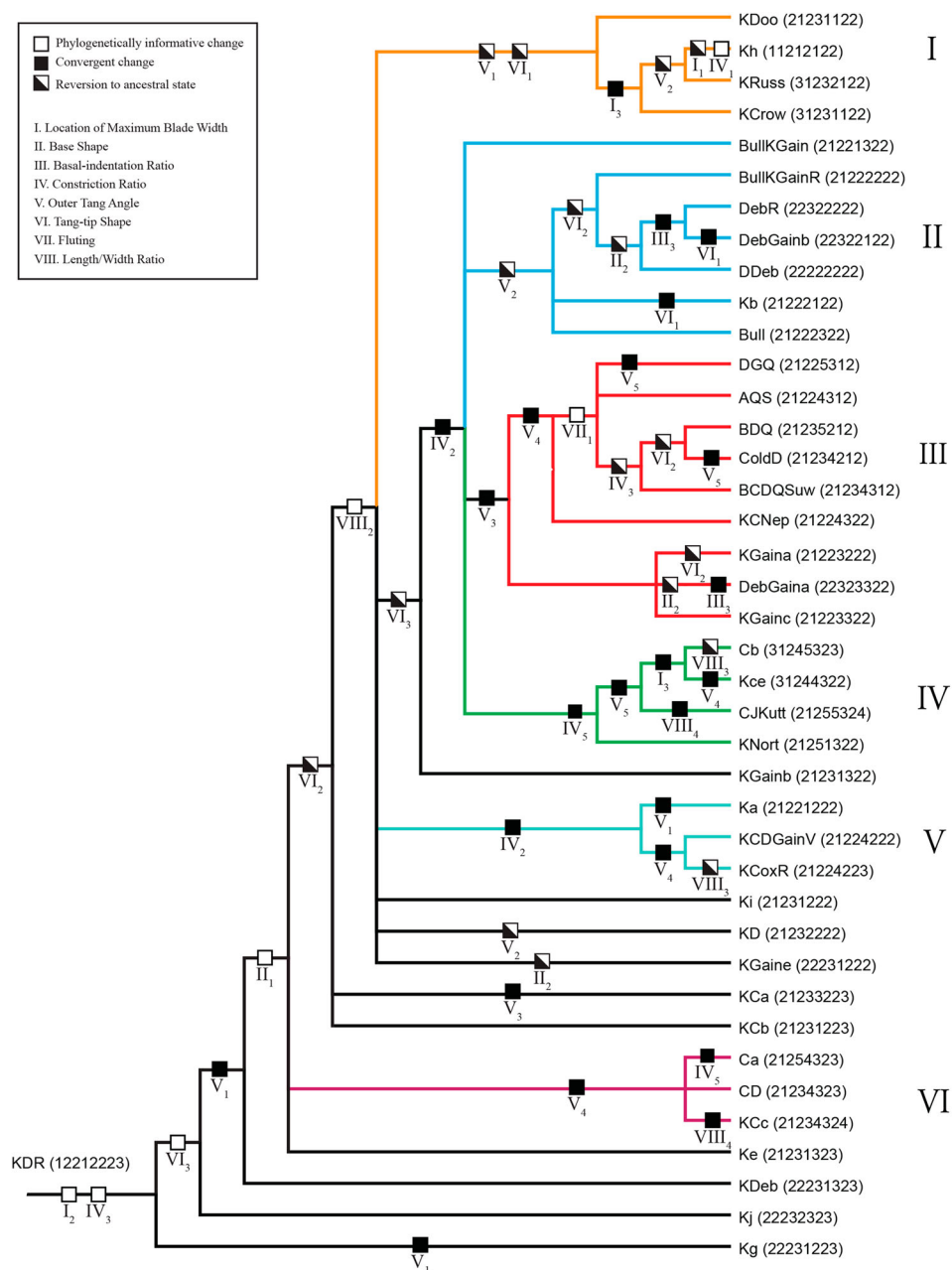


Figure 7 Fifty-percent majority-rule consensus tree of 41 taxa based on 100 replicates. The boxes show the 48 changes in character states. Roman numerals denote characters, and subscript numbers denote character states. Open boxes indicate phylogenetically informative changes; shaded boxes indicate parallel or convergent changes (homoplasy); and half-shaded boxes indicate characters that reverted to an ancestral state. Clades I–VI are shown in different colors (from O'Brien et al. 2014).

classification is what is illustrated in Figure 3, where the character states of three characters create 12 classes ($2 \times 3 \times 2$). Before starting a paradigmatic classification, the investigator specifies the characters and the states of each character that might be of analytical interest. There is no limit to the number of characters and states that can be included. Each specimen is then classified by noting the states of each character. Any state belonging to a single character can combine with any state belonging to any other character. Whether they actually do or not in a particular collection of specimens is a separate, empirical question (O'Brien and Lyman 2000, 2002b).

Paradigmatic classification escapes a major problem with standard typology, namely, the lack of redundancy in the characters used to create types. In the case of projectile points, one point type may be defined primarily by blade length and curvature, whereas another point type may be defined by basal shape and curvature. As O'Brien, Darwent, and Lyman (2001) note, one might argue that in biology species are nonredundant in terms of definition, especially in cases where morphological characters are used as sorting criteria, and yet they constitute the taxa often used in cladistics. We agree with this assessment, but the lack of redundancy in species

definitions is no warrant for introducing the problem into archaeological systematics (O'Brien and Lyman 2000). To be clear, we are not claiming that there is no role in archaeology for extensionally derived units such as point types. As shorthand mnemonic devices they serve a useful purpose in conveying coarse-grained information that aids communication. They are not, however, robust enough to use in the kinds of analysis reported here (O'Brien et al. 2014).

Common to our studies of eastern North American Paleoindian points was the use of a suite of eight characters to define projectile-point classes (Fig. 6). The choice of which characters to use was based on expectations as to which parts of a point would change most over time as a result of cultural transmission and thus create a strong phylogenetic signal (O'Brien, Darwent, and Lyman 2001). As we noted earlier, archaeologists, like biologists, lean heavily on experience in selecting characters, and our experience with Paleoindian points, in conjunction with published studies (e.g., Musil 1988), suggested that the hafting element is a likely region in which to find other characters that would be useful in phylogenetic analyses. The haft area, as Thulman (2006) notes, is perhaps also the least likely to have been altered from its original form since manufacture, although this does not necessarily apply to Clovis points (Buchanan et al. 2012, 2015). Four characters—II, III, V, and VI—were selected to monitor changes in such features as base shape, the shape of tang tips, and the angle formed by a tang relative to the long axis of a specimen. Considerable variation exists in the size and shape of Paleoindian points, so we selected characters I, IV, and VIII in order to explore those changes.

Here, class definitions are eight-character number strings. For example, referring to the characters and character states in Figure 6, class 21224222 would be defined as having its maximum blade width in the secondmost proximal quarter (I_2); an arc/round base (II_1); a shallow basal-indentation ratio (III_2); a constriction ratio of 0.90–0.99 (IV_2); an outer tang angle of 66° – 80° (V_4); a round tang-tip shape (VI_2); fluting (VII_2); and a length–width ratio of 2.00–2.99 ($VIII_2$). Because it is much easier to use class abbreviations than it is to write out class definitions (the number strings)—not to mention easier to remember—we use them in discussions below. Note that the abbreviations are based on commonly used type names, which in each case were taken directly from the literature in which the specimens were illustrated. For example, Class KCDGainV contains at least one specimen that was originally referred to as a Clovis (K) point, at least one as a Cumberland (C) point, at least one as a Dalton (D) point, at least one as a Gainey (Gain), and at least one as a Vandale (V) point. Echoing our earlier point, this ought to give us pause the next time we think about using traditional projectile-point types as analytical units (O'Brien and Lyman 2002b).

The Consensus Tree

The analysis discussed here focused on 1113 points from across the East (O'Brien et al. 2014). Our classification resulted in a total of 763 classes, each representing a filled segment of design space, from which we selected a subset of classes that contained four or more specimens each. This created a subsample of 218 specimens spread over 41 classes. The number four has no significance; as in previous studies, we

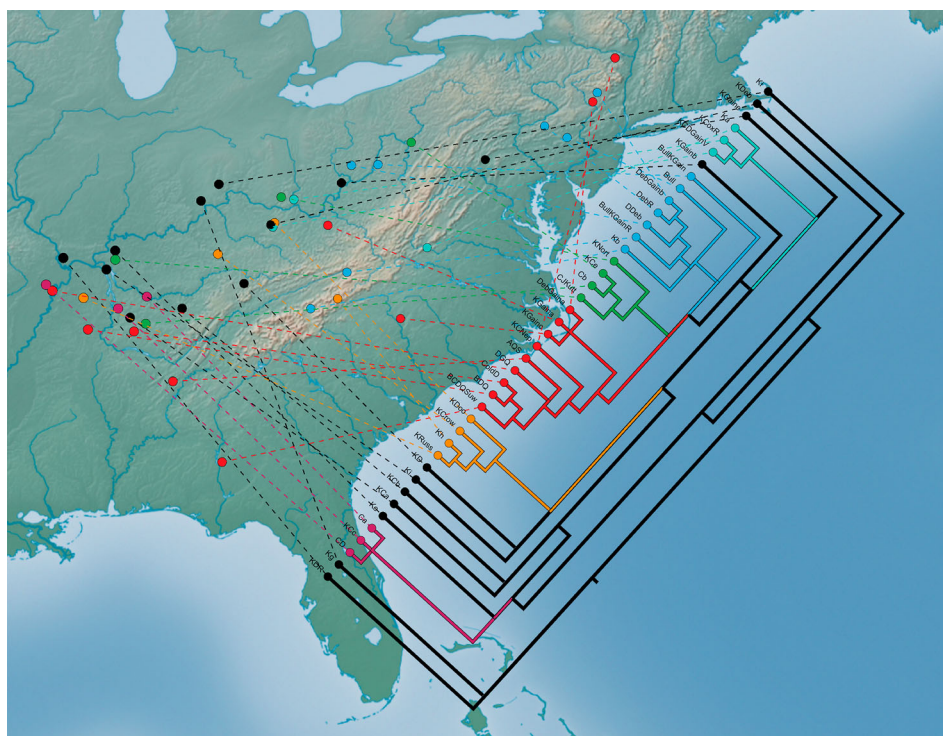


Figure 8 Geographic distribution of clades (from O'Brien et al. 2014).

used it solely as a means of controlling for idiosyncrasies arising from such things as individual skill level and occasional mistakes. This yields a conservative number of taxa and allows us to examine the spatial distribution of specimens within a taxon. The majority-rules consensus tree, shown in Figure 7, contains 48 character-state changes, represented by boxes. Each box is labeled with a Roman numeral indicating the character that has changed; the subscript Arabic numeral indicates the evolved character state. White boxes indicate phylogenetically informative changes—shifts that result from descent with modification as opposed to changes that result from either adaptive convergence (black boxes) or a reversal to ancestral character states (half-shaded boxes). As discussed earlier, the latter two kinds of change are not useful in tracing phylogeny, but they do provide information on the kinds of subtle variation present. The tree exhibits numerous clades—again, a grouping defined as two or more related taxa and their common ancestor—some of which are labeled I–VI.

Geophylogenetic Distribution of Classes

Projecting the consensus tree into geographic space, creating a *geophylogeny*, allows us to observe the significance of the phylogeny in both time and space (Fig. 8). In particular, a geophylogeny serves as an independent test of the validity of a phylogenetic hypothesis because it allows us to determine whether an ancestor–descendant pair of taxa are in spatial proximity to one another. If they are not, then we likely have not measured phylogeny but something else. To construct the projection, O'Brien and colleagues (2014) calculated the mean geographic centroid of the county in which each specimen was obtained, then used the coordinates to calculate a spatial envelope representing the geographic distribution of each class. The spatial centroids were then calculated to create a weighted mean representing the center point of each class's distribution.

Classes in Clade I (orange in Fig. 7) all contain specimens identified as Clovis (K) points and are located primarily in the Midwest and Upper Midwest. Classes in Clade II (blue) are skewed toward the Northeast and Middle Atlantic regions. Key constituents of the classes are projectile-point types—Bull Brook (Bull), Gainey (Gain), Debert (Deb), Clovis, and Redstone (R)—described in the literature as having deep basal indentations (MacDonald 1968; Robinson et al. 2009). Several studies have shown that relative depth of the basal indentation varies widely across time and space, with the deepest indentations being in the Northeast and around the Great Lakes (Miller and Gingerich 2013; O'Brien, Boulanger, et al. 2015). Classes in Clade III (red) show a split distribution: Two classes occur in the Northeast, which is not surprising, given that a key constituent of the subclade is Gainey, a point type (or subtype) that occurs primarily along the southern edge of the Great Lakes eastward, although it is found sporadically throughout eastern

North America (Gramly 1982). Five other classes extend in a band from the Midwest into the Southeast; one occurs in the Upper Midwest; and another occurs in the Mid-Atlantic region. Classes in Clade IV (green) occur in a band from the Tennessee River valley north-eastward, generally following the Ohio River. This is also not surprising, given the large number of Cumberland points, a key component of classes in Clade IV, that are found in the Tennessee and central Ohio River valleys (Anderson et al. 2010). Classes in Clade V (light blue), all of which contain Clovis points, occur in the Upper Midwest—primarily along the Ohio River—and toward the Mid-Atlantic region. Classes in Clade VI (magenta), all containing Cumberland points, cluster in the Midwest eastward to the Tennessee River valley. In terms of position, Clade VI extends well back into the tree; it split off at the same time as the ancestor (Ke) that produced all other clades.

Of particular interest are the 11 unresolved classes—those that do not fall into one of the six clades—represented in black in figures 7 and 8. In their classic model of Clovis colonization of North America, Kelly and Todd (1988) suggest that the speed of colonization was driven by high rates of residential mobility because of the large foraging areas required of a primarily carnivorous diet. Hamilton and Buchanan (2007) note that Clovis colonists would have moved rapidly through large river systems such as the Missouri, Mississippi, and Ohio drainages, leading to an initially rapid rate of colonization through the midcontinent, which would have then slowed dramatically as diet breadths broadened with the increased biodiversity of the eastern forests (Steele et al. 1998) and as prey size, abundance, and availability changed (Meltzer 1988).

Note the locations of the unresolved classes: They occur in the Upper Midwest near the junction of the Mississippi and Ohio rivers, northeastward along the Ohio River, and southeastward along the Cumberland River. All 11 classes, including the two outgroups, contain specimens identified in the original literature as Clovis points. In some cases, all specimens were identified as Clovis, and in others some were classified as Gainey, Cumberland, Redstone, Debert, and/or Dalton. A working hypothesis based on this distribution would be that the unresolved classes were the products of groups moving rapidly across the landscape—so rapidly that there was not enough time for a strong phylogenetic signal to develop (O'Brien, Boulanger, et al. 2015). There were technological changes, but there were too few to allow much resolution of phylogeny. If, as we propose, the unresolved classes are associated primarily with Clovis groups, then a related proposal is that the more-resolved classes, those in clades II–IV, represent later Early Paleoindian points (O'Brien et al. 2014).

Clovis Social Interaction

What, if anything, might these distributions tell us about social interaction among Clovis groups? As

background, we can turn to a study by Sholts and colleagues (2012; see also Gingerich et al. 2014), who examined flake-scar patterns on a sample of Clovis points from sites across North America and found that flaking patterns were similar, “without evidence for diversification, regional adaptation, or independent innovation” (3024). Sholts and colleagues proposed that learning how to make Clovis points could have taken place at chert outcrops—quarry sites—where “Clovis knappers from different groups likely encountered each other ... [which] would have allowed knappers to observe the tools and techniques used by other artisans, thereby facilitating the sharing of technological information.” This sharing of technological information, Sholts and colleagues proposed, created the uniformity in production seen in their sample. If they are correct, then regardless of whether variation in shape is attributable to the vagaries of cultural

transmission (drift) or adaptive change driven by environmental conditions (selection), patterns of flake removal appear to have been less likely to change than shape was.

Eren, Buchanan, and O'Brien (2015) tested the hypothesis using a sample of Clovis points from one environmentally homogeneous region of the Midcontinent centered on the Ohio River valley. The 115 points were made from cherts from the three principal outcrops in the study area: Wyandotte, Indiana; Hopkinsville, Kentucky; and Upper Mercer, Ohio (Tankersley 1989). Analysis of flake-scar patterning confirmed that the production technique was the same across the sample but that there were differences in point shape associated with the stone outcrop from which particular Clovis points originated. If stone outcrops were hubs of regional Clovis activity (Sholts et al. 2012), the results of the study by Eren and

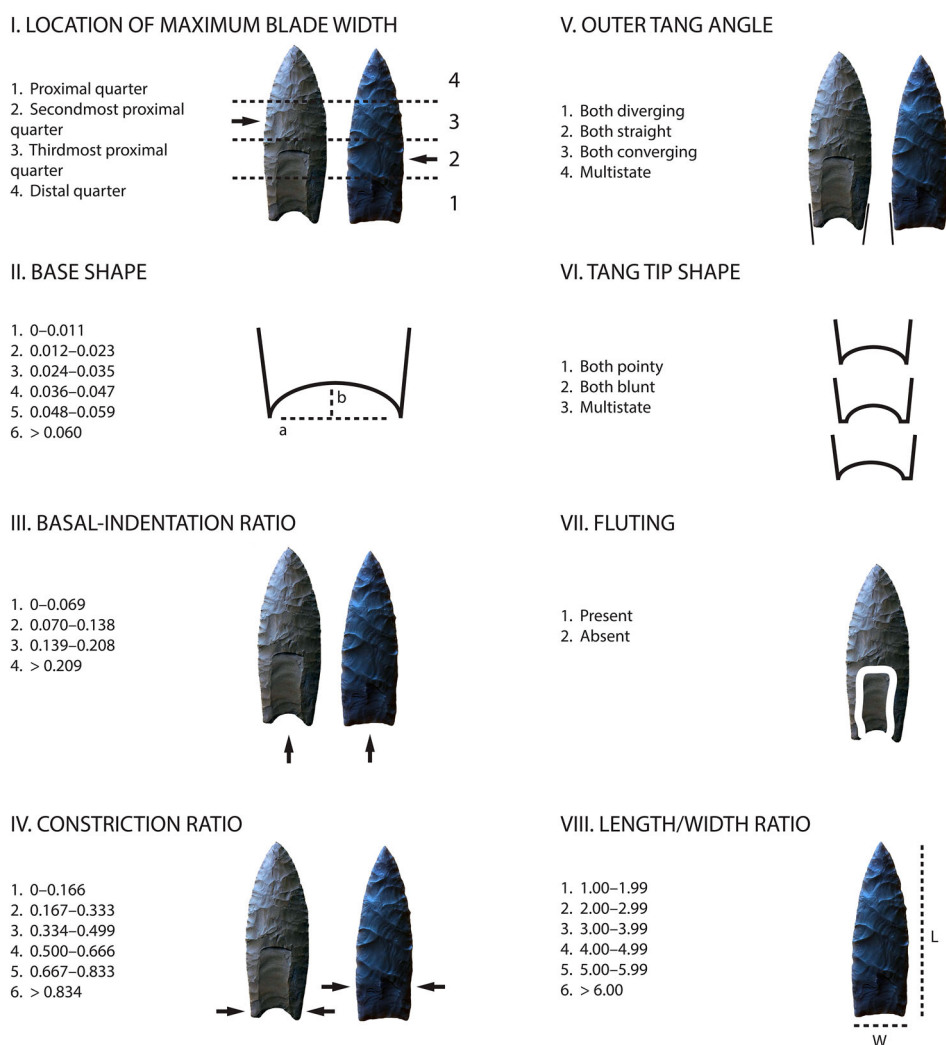


Figure 9 Characters and character states used in the analyses of Clovis points from Ohio, Indiana, and Kentucky. Recording of characters I, III, IV, VII, and VIII follows O'Brien et al. (2014). Character II (base shape) was measured using Collins's (1999) index of curvature. Character states in character V (outer tang angle) were determined as follows: if both tangs are greater than 92 degrees the character is “diverging”; if both tangs are less than 88 degrees the character is “converging”; if both tangs are between 88 and 92 degrees the character is “straight”; if the tangs differ in the above categories the character is “multistate.” Character VI (tang tip shape) was measured by treating the tangs as “spurs” and determining the pointy or blunt status following the procedure of Eren, Jennings, and Smallwood (2013).

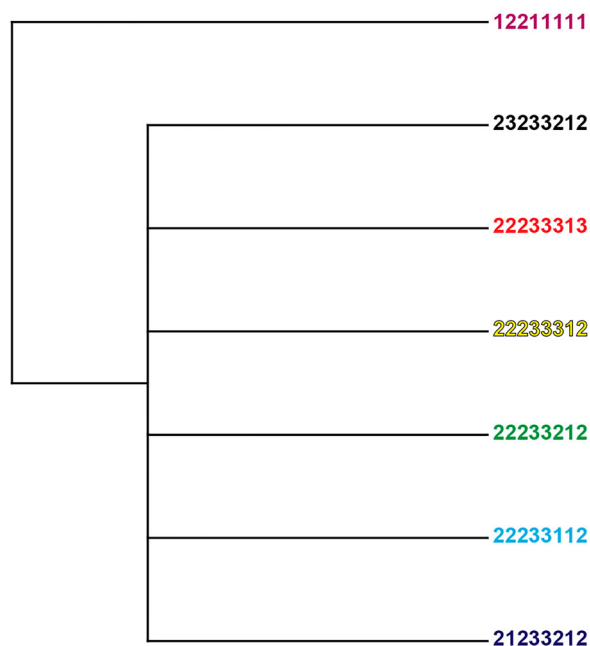


Figure 10 Majority-rules consensus tree for seven projectile-point classes containing Clovis points from Ohio, Indiana, and Kentucky.

colleagues confirm that Clovis foragers engaged in two tiers of social learning. The lower, ancestral, tier relates to point production and can perhaps be tied to conformist transmission of ancestral tool-making processes across the Clovis population, although that proposition has not yet been tested (see Crema et al. 2014). In other words, dispersing Clovis groups were still socially connected across large regions of North America and directly transmitting technological knowledge to each other, resulting in a low interregional variation in how points were being flaked. The upper, derived, tier relates to point shape, which shows more interregional variation. Because Eren, Buchanan, and O'Brien's (2015) analysis was at a regional level, where environment was relatively homogenous, the point-shape differences can be tied not to environmental adaptation but rather to drift that resulted from individual groups spending more time at different stone-outcrop hubs.

When we said that point shape began to drift, we need to make clear that the drift is evident at the megapopulation level, as Clovis groups began to drift apart, not at the local-group level. At the group level, the apparent pattern of increased experimentation in shape is what we would expect from the guided-variation model, where in the absence of selection, a population will move toward whichever trait is favored by people's individual-learning biases (Gingerich et al. 2014; Mesoudi 2011; O'Brien, Buchanan, et al. 2015; O'Brien et al. 2014). We propose that this regionalization parallels the findings of several studies that have noted increasing projectile-point diversification and shrinking "style zones" in the time period immediately following Clovis (post-ca. 12,500 calBP)

(Anderson 1995; O'Brien, Boulanger, et al. 2015; O'Brien et al. 2014; Tankersley 1989). Meltzer (2009, 286) suggests, and we agree, that this process can be read "as a relaxation in the pressure to maintain contact with distant kin, a reduction in the spatial scale and openness of the social systems, and a steady settling-in and filling of the landscape. Later Paleoindians no longer spanned the continent as their ancestors had, and their universe had become much smaller."

Having determined that point-shape differences in the sample of Clovis points from the Ohio–Kentucky–Indiana region were tied to drift that resulted from individual groups spending more time at different stone outcrops, we carried out a cladistic analysis to determine whether we could detect a phylogenetic signal in those data. This issue has implications for tracking and linking individual bands of Clovis foragers as they moved into new regions as well as for the tempo of their colonization movements. The sample of points we analyzed earlier (see above) was expanded to 244 specimens (Supplemental Material 1).

We classified the points using the paradigmatic classification described earlier (Fig. 6), but with a few minor changes in how character states were measured (Fig. 9). The Paleoindian-point samples used in previous analyses contained a wide variety of shapes, given that they were from much or most of eastern North America and included both Clovis points and points that immediately postdated Clovis. Given the more restrictive temporal and geographic range of the Upper Midwest sample—recall that all the specimens were referred to by Tankersley (1989) as Clovis points—there was significantly less shape variation

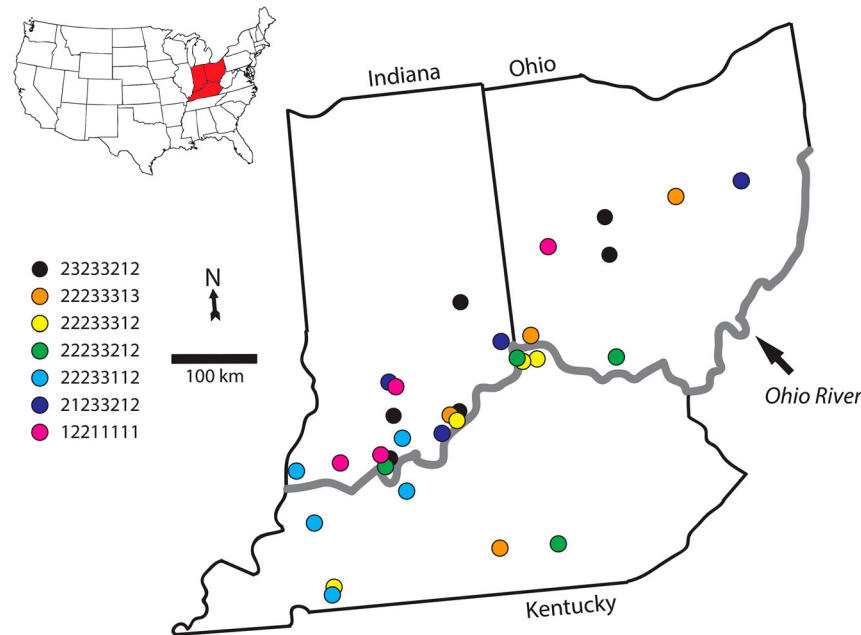


Figure 11 Geographic distribution of specimens in the seven projectile-point classes shown in Figure 10.

and thus we could focus on more-minute variation among character states. The modified classification meant there were 82,944 classes, of which 176 were represented in the sample of 244 points. Following previous protocols (O'Brien et al. 2001, 2014), we selected a subset of those classes that contained four or more specimens ($n = 7$), accounting for 31 specimens. Again, the use of taxa with four or more specimens was merely a way of controlling for idiosyncrasies arising from the multiple sources of variation that could potentially influence discarded points: knapper skill, time budgeting, breakage, and the like (Lycett and von Cramon-Taubadel 2015).

Again, we used PAUP* (v. 4) (Swofford 1998) to create the tree. The branch-and-bound search routine we used, as in all previous analyses (O'Brien and Lyman 2003), produced eight equally parsimonious trees and the majority-rule consensus tree shown in Figure 10. It has a CI of 0.8571 and an RI of 0.7143—high figures but not surprising in light of the fact that the consensus tree has a polytomy (a non-bifurcating branch) comprising six of the seven point classes. The remaining class (12211111) forms a branch of its own. Based on the limited data available, that class (shown in magenta in Figs. 10 and 11) is ancestral to the others. As such, note that it has four character states not evident in the other taxa: (1) its maximum blade width is in the proximal quarter (I_1); (2) it has a constriction ratio of 0–0.166 (IV_1); (3) it has outer tang angles that both diverge (V_1); and (4) it has a length/width ratio of 1.00–1.99 ($VIII_1$). No other class has more than one unique character state. Are we seeing the first “Clovis” point class east of the Mississippi River? Only much larger samples will allow us to test that proposition.

The lack of a strong phylogenetic signal—signified by the lack of branching—can be explained in one of

two ways. First, it is possible that because the sample consisted entirely of Clovis points and hence morphological variation was low, a more comprehensive morphometric scheme could tease out a phylogenetic signal that the current eight characters are missing. Alternatively, the lack of a strong phylogenetic signal may be pointing to the fact that although significant evolutionary changes are emerging, as evidenced by the point-shape patterning detected by Eren, Buchanan, and O'Brien (2015), those changes are simply not pronounced enough to differentiate the six classes. This second possibility has an important behavioral implication of its own, namely that the absence of a strong phylogenetic signal is consistent with the inferred speed with which Clovis foragers colonized the Ohio–Indiana–Kentucky region of the midcontinent specifically and the rest of the continent more generally (Meltzer 2009; Waters and Stafford 2007). Taken together, these two details suggest that the distribution of Clovis points across the region itself must have occurred rather quickly, speculatively perhaps in two to four generations (50–100 years).

The geographic distribution of specimens is shown in Figure 11. Despite the small sample size, there appears to be rough geographic clustering of some point classes. Class 22233112 (light blue) forms a fairly tight cluster in the southwestern part of the region, whereas class 22233212 (green) forms a cluster in the south central and southeastern part. It is worth noting that in each class specimens appear either around the Ohio River and south of it (light blue, green, and yellow) or around the Ohio River and north of it (magenta, dark blue, and black). Only one class—22233313 (orange)—breaks this pattern, but it is only a single point that is an outlier. Broadly, these results are consistent with those of Eren, Buchanan, and O'Brien (2015) and further support the notion

that drift is occurring at the Clovis megapopulation level, although, to reiterate, the sample is small.

Conclusions

As we have noted on several occasions (e.g., O'Brien et al. 2012, 2013), the growing interest in cultural phylogenetics witnessed over the last couple decades marks a return to the questions on which the founding of much of anthropology rests: the writing of cultural lineages (Lyman, O'Brien, and Dunnell 1997). This return is important to the growth and continued health of anthropology because a reconstructed phylogeny helps guide interpretation of the evolution of traits in that it generates hypotheses about the lineages in which those traits arose and under what circumstances (Linder and Rieseberg 2004). Cladistics is one method that is particularly well suited for analyzing lineages because it relies only on shared derived character states to create hypothetical statements of ancestor–descendant relationships. It is difficult to overemphasize that cladistics is not a biological method that depends on genetic continuity as a basis for reconstructing phylogeny. Rather, it depends on transmission, regardless of kind. Archaeological materials were at one time parts of human phenotypes in the same way that shells, teeth, and fossilized bones were (O'Brien and Holland 1995). If there is phenotypic change in, say, projectile points, and if over time enough variation is generated, cladistic analysis might indeed be able to detect the phylogenetic signal. If so, we should be able to create a phylogenetic ordering that has testable implications.

Our example of Paleoindian projectile-point evolution in eastern North America represents roughly 15 years of interrelated analyses geared toward understanding social interaction across the landscape. The first study (O'Brien et al. 2001) was, to our knowledge, the most comprehensive look at how to integrate cladistics into archaeology. This is not to ignore earlier insights made by others (e.g., Foley 1987), but that study demonstrated not only how to conduct a phylogenetic analysis on a large data set but how to create appropriate analytical units—again, with “appropriate” being defined in terms of how well a unit performs in allowing us to separate taxa phylogenetically. Later studies focused on how phylogenies could be used to examine questions about cultural transmission among Paleoindian groups as they colonized the East and began to settle into specific regions. The first phylogeographic analysis (O'Brien and Lyman 2003) was limited by a small sample, which was expanded to cover much of eastern North America (O'Brien, Boulanger, et al. 2015; O'Brien, Buchanan, et al. 2015; O'Brien et al. 2014). We then turned attention to one region of the Upper Midwest (Boulanger et al. 2015; Eren, Buchanan, and O'Brien 2015) to see if we could track the flow of social information across the landscape and determine the kinds of social interactions that were taking place. Results presented in

this paper support the notion that drift is occurring at the regional level, resulting from individual groups spending more time at different stone outcrops.

In conclusion, we emphasize a point we have made time and again (e.g., O'Brien et al. 2013, 2014): Phylogenetic methods are but one tool in the archaeologist's toolbox—an important one, but one that cannot be applied haphazardly to any data set. Other tools useful in phylogenetic analysis include seriation—especially occurrence seriation (O'Brien, Darwent, and Lyman 2001; O'Brien and Lyman 1999; O'Brien et al. 2002)—and network analysis (Cochrane and Lipo 2010; Jordan 2015; O'Brien, Boulanger, et al. 2015), which is useful for identifying complex transmission histories of cultural convergence and divergence (Ross, Greenhill, and Atkinson 2013). Finally, at the risk of annoying the reader, we reiterate that phylogenies are not end products in themselves; rather, they are solid starting points from which to begin to answer some of archaeology's historical, and therefore evolutionary, questions.

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